Recognizing a new species of *Silene* (Caryophyllaceae) from California: a splitter’s game?

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*Silene krantzii* T.R. Stoughton is a new species endemic to higher elevation, alpine habitats in the San Bernardino Mountains, San Bernardino County, California. The new species appears to be abundant in locations where it has been observed, but it is narrowly restricted in overall distribution, presumably due to the limited availability of suitable habitat. *Silene krantzii* sp. nov. is morphologically similar to a closely related species in the San Bernardino Mountains, *Silene verecunda* S. Watson, but differs from this taxon in the San Bernardino Mountains by the presence of glandular trichomes on the basal leaves and proximal stems, smaller leaf size, a red calyx that is inflated at flowering, and a short-statured, spreading habit. *Silene krantzii* also occurs in a unique ecological setting. Qualitative evidence of these differences is summarized for the new species and relevant information regarding ongoing study of genetic diversity within the *S. verecunda* complex is discussed.

Key words: alpine, catchfly, morphology, natural history, San Bernardino Mountains, San Gorgonio Mountain, *Silene krantzii, Silene verecunda*, Southern California, species concepts

Over the course of multiple botanical forays to the alpine zone of San Gorgonio Mountain, located in the San Bernardino Mountains, California, several plants resembling *Silene verecunda* S. Watson (1875) were collected by the first author. All known specimens previously identified as *Silene verecunda* subsp. *platyota* (S. Watson) C. L. Hitchcock & Maguire (1947) from subalpine (<3,000 meters), mixed conifer forests of the San Bernardino Mountains held at RSA/POM and UC/JEPS herbaria were examined. We observed several distinct differences between *S. verecunda* subsp. *platyota* and the unidentified *Silene* collections from the alpine zone of San Gorgonio Mountain. We now propose that these differences are sufficient to recognize the populations on San Gorgonio Mountain as a
new species of Silene in the San Bernardino Mountains, utilizing a taxonomic concept proposed by Cronquist (1978) in which taxa are circumscribed based on discontinuity of morphological features. Natural history information included here lends additional support for the recognition of a new species of Silene endemic to the San Gorgonio summit region of the San Bernardino Mountains drawing on aspects of more contemporary species discourse recently articulated by Baum (2009).

**Taxonomy**

*Silene krantzii* T.R. Stoughton, sp. nov. (Figures 1–4).—TYPE: USA, California, San Bernardino Mountains, ‘The Tarn’ just below (south of) the San Gorgonio summit region (Figure 1A), alpine gravel fell-field with *Festuca saximontana, Raillardella argentea, Calyptridium umbellatum, Hulsea vestita* subsp. *pygmaea* and *Elymus elymoides*, granitic substrates, 3,272 m elev., 34° 5’ 34.37” N, 116° 49’ 23.30” W, 23 July 2011, Thomas Stoughton 1391, with R. Shores, M. Seccombe, and P. Boyd (Holotype: RSA806300; Isotypes: GB, JEPS, CAS, NY, UCR).

![Image](image_url)

**Figure 1.**—*Silene krantzii* in native habitat. A. Alpine fell-field habitat at the type locality, “The Tarn” just below the south face of San Gorgonio Mountain in the San Bernardino Mountains, San Bernardino County, California. B. Overall plant habit demonstrating prostrate nature of stems and racemose inflorescences. C. Flower displayed in side-view, showing inflated and ribbed condition of the mature calyx in flowering. D. Basal leaves and stems, showing oblongulate shape and presence of glandular trichomes. Photographs by Thomas R. Stoughton.
Figure 2.—Distribution of the Silene virecunda complex.  A-B.  Locality information downloaded from the Consortium of California Herbaria and Intermountain Regional Herbarium Network.  A.  The easternmost taxon in the S. virecunda complex (circles) is subsp. andersonii (Clokey) C. L. Hitchcock & Maguire, whereas the majority of the morphological variation exhibited by this species is attributed to subsp. platyota (S. Watson) C. L. Hitchcock & Maguire in the Sierra Nevada, Transverse Ranges and Peninsular Ranges of California (including Baja, MEX). Plants from the Coast Ranges of California represent the 'typical' variety, with the type specimen for S. virecunda S. Watson reported from serpentine substrates on Mt. Davidson in the San Francisco Bay Area.  B.  Inset showing the Transverse and Peninsular Ranges of southern California, with the location of S. krantzii (stars) on San Gorgonio Mountain indicated in the southern portion of the San Bernardino Mountains, San Bernardino County, California.
Caespitose perennial herb, caudex branches few to many below ground, many fertile shoots at the base 2–10(14) cm long, spreading to ascending, generally unbranched, glandular-viscid throughout, hairs generally less than 0.5 mm, glands stipitate. Basal leaves linear-oblanceolate, (5)8–30 × 1–3 mm, apex acute, base attenuate into short petiole, both surfaces glandular-viscid, 1-veined or venation obscure, in opposite pairs of 2. Cauline leaves similar to basal leaves, but gradually reduced apically, linear-lanceolate, few, sessile, often with fertile axillary branches, opposite. Inflorescence generally an open cyme, monochasial (generally not a compound dichasium), 1–4 flowered with ascending branches. Bracts linear-lanceolate, margins membranaceous. Peduncles 0.5–2.5(3.5) cm long. Bracteoles similar to cauline leaves, but lanceolate-ovate and gradually smaller than bracts. Pedicels up to 2.5(3.5) cm long, generally longer than calyx. Calyx 10-nerved, 8–15 mm long, cylindrical-campanulate to campanulate-clavate, narrowed proximally around carpophore, reddish, densely glandular-viscid, generally somewhat inflated at flowering with pale commissures between prominent parallel veins, not clearly papery in fruit; teeth keeled, broadly ovate to triangular, ca. 1–3 × 1–1.5 mm, obtuse, with membranaceous and ciliate margins. Carpophore ca. 0.5–1(1.5) mm long, hairy. Petals pink, (7)9–17 mm long; limb broadly obovate, ca. 2.5–4 mm long, distinctly divided to ca. 2/5 total length; lobes broadly oblong, ca. 0.5–1.5 x 0.5 mm, margins lacinate at base; claw elliptic-oblong to obovate, slightly exserted beyond calyx, ca. (5)6–9(10) × 0.3–1.2 mm, ciliate near base; coronal scales 2, oblong, 0.5–1.5(2) mm long, rounded at tip or toothed, sometimes with lacinate margins. Stamens exserted from the calyx but ± equal to corolla, styles slightly more exserted; filaments usually sparsely pilose proximally. Styles 5.5–8 mm long. Capsules narrowly elliptic-obovate to clavate, (5.5)7–10 × 4–5.5 mm, included in the calyx. Seeds brownish, usually orbicular-reniform to oblong, 1–1.5 mm long, flattened, papillate-tuberculate with papillae developed into a low crest along margin.
Figure 4.—Silene krantzii. Scan of the type specimen, Stoughton et al. 1391 (RSA806300), collected from “the Tarn” in the San Gorgonio Wilderness, San Bernardino National Forest, San Bernardino County, California.
Silene krantzi is morphologically similar to the broad interpretation of S. verecunda. S. Watson by Morton (2005) in some respects, but differs in its ecological setting and the presence of glandular trichomes on the basal leaves and proximal stems, smaller leaf size, a red calyx that is inflated at flowering, and a low-susurate, spreading habit.

Silene krantzi is typically found on sand or gravel substrates of primarily igneous origin. Most records describe it in open, exposed areas above tree line with mixed shrubs and herbs (including Festuca saximontana, Rarrardella argentea, Hulsea vestita subsp. pygmaea, Calyptridium umbellatum, and Elymus elymoides), although some records describe the habitat as rocky rather than sandy or gravelly. The species is cited as being scarce to common in different localities and habitats around the summit region of San Gorgonio Mountain, but personal observations by the first author suggest it is densely abundant at the type locality and in other areas around the summit region of San Gorgonio Mountain. That said, S. krantzi is thus far known only from high elevation (3000–3500 m) locations in the San Bernardino Mountains of southern California. Plants flower from as early as mid-May to as late as early September and develop mature fruits from June to October.

The specific epithet, krantzi, refers to the first author’s botanical mentor and friend, Timothy Krantz, who has greatly enriched our knowledge of the flora of the San Bernardino Mountains (Krantz 1994). The suggested common name for the species is Krantz’s catchfly.


**Taxonomic Relationships**

Silene krantzi appears to be a close relative of Silene verecunda S. Watson (1875), a staggering variable species of Silene that is widespread in southwest North America. Silene verecunda (Figure 5) occurs in California, Nevada, Utah, Arizona, and in Baja California, Mexico (Morton 2005), with unsubstantiated reports of the species from Oregon. Disregarding all subspecies in the most recent treatment, Morton (2005) suggested that separation of taxa would be arbitrary and that the species complex is in need of in-depth study. Despite this conclusion, Morton provides numerous morphological characters and disparate ecological settings for distinguishing taxa associated with the group. Morton’s taxonomic concept of Silene is in direct contrast to later findings of Popp and Oxelman (2007), who used base pair substitutions from both nuclear and plastid markers to assess relationships among many members of Silene in North America. Popp and Oxelman (2007) found Silene andersonii Clokey [= S. verecunda subsp. andersonii (Clokey) C. L. Hitchcock & Maguire] to be resolved in a separate clade than that of two other accessions of S. verecunda they included in their analyses. A more recent study (Petri and Oxelman 2011) further substantiates paraphyly of S. verecunda as circumscribed by Morton (2005). This suggests that some of the morphological variation observed by previous authors (Watson 1875, 1882, 1888; Jepson 1914; Clokey 1939; Hitchcock and Maguire 1947) may
Figure 5.—Silene verucunda subsp. verucunda in native habitat near the type locality of S. verucunda S. Watson on Mt. Davidson, in the vicinity of San Francisco Bay, California. A. Overall plant habit demonstrating decumbent to erect nature of the stems of these considerably larger plants. Silene verucunda subsp. verucunda occupies coastal, lower elevation habitats in California, which is in stark contrast to the inland, alpine habitat of S. krantzii. B. Basal leaves and stems, showing oblongolate shape with much more pronounced petioles compared to S. krantzii. Silene verucunda subsp. verucunda does exhibit glandularity on the proximal stems and leaves like S. krantzii, but these trichomes are larger, less-dense, and of a different structural arrangement. C. Flower displayed in side-view, showing somewhat inflated condition of the mature calyx in flowering similar to S. krantzii. Note that calyces are considerably less red in color than S. krantzii and a noticeable keel on the calyx teeth is lacking. Photographs used by permission from Scott Simono, San Francisco State University, California.

have a genetic basis and that the associated ecological affinities may represent locally adapted genotypes (with corresponding morphotypes) rather than phenotypic plasticity in a widespread, generalist species.
Qualitative Analyses and Classification

Specimens of all members of the *S. verecunda* complex (including *S. krantzii*) from herbaria at RSA/POM and UC/JEPS were examined (Appendix I) as part of a larger project (T. Stoughton et al., Rancho Santa Ana Botanic Garden, unpublished data) evaluating the taxonomic validity of the previously recognized subspecies of *S. verecunda* using molecular phylogenetics. A total of 130 specimens of *S. verecunda* s.l. (Morton 2005) collected from California (including Baja) were examined, including 82 specimens of *S. verecunda* subsp. *platyota* and 11 specimens of *S. krantzii* collected from the San Bernardino Mountains. A limited number of representative specimens for the other subspecies of *S. verecunda* outside of the San Bernardino Mountains are listed in Appendix I, including 9 specimens of subsp. *andersonii*, 20 specimens of subsp. *platyota*, and 8 specimens of subsp. *vere cunda*.

We considered treating the new taxon as a variety or subspecies of *S. verecunda* because, like *S. verecunda* s.l., it is ciliate on the petal claw with two petal limb lobes that have laciniate margins. *Silene krantzii* overlaps morphologically with *S. verecunda* s.l. in portions of its geographic range in several other features. The branching pattern of *S. krantzii* is similar to that of *S. verecunda* subsp. *platyota*, but the primary axes of *S. krantzii* are generally more prostrate to spreading in comparison and *S. verecunda* subsp. *platyota* tends to have inflorescences that are compound dichasium. Plants of *S. krantzii* are smaller than *S. verecunda* subsp. *platyota*, which occurs at lower elevations in the San Bernardino Mountains (below 3,000 m). The range of corolla size among *S. krantzii* plants is similar to that of *S. verecunda* s.l. Seeds of *S. krantzii* appear to be smaller than that of *S. verecunda* s.l., but are similar to the latter species in being flattened, papillate-tuberculate, and orbicular-reniform to oblong in shape with papillae that are developed into a low crest along the margin. The principal distinction between *S. krantzii* and the subspecies of *S. verecunda sensu* Hitchcock and Maguire (1947) is the unique combination of: (1) glandular trichomes on the basal leaves and proximal stems; (2) leaves of reduced size; (3) a red calyx that is inflated at flowering; and (4) a low-stature, spreading habit (see Appendix II, Key to *Silene verecunda* species complex). These distinctive morphological features of *S. krantzii*, along with its isolated geographic distribution in the alpine zone of the San Bernardino Mountains having no known intergradation with *S. verecunda* s.l., warrant its species status by a taxonomic (morphologic) species concept (Cronquist 1978) that incorporates information regarding natural history of the species.

Physical isolation of *S. krantzii* populations at high elevation in the San Bernardino Mountains region and the evolution of unique morphological and ecological features suggest that this species has either a restricted niche, limited dispersal ability, or both. In general, we know very little about the phylogenetic relationships within the *S. verecunda* complex (Popp and Oxelman 2007, Petri and Oxelman 2011), so gaining a better understanding of these relationships should be the goal of future molecular studies of California *Silene* species. Although no explicit attempts have been made to characterize genetic diversity in the group, recent research (Popp and Oxelman 2007, Petri and Oxelman 2011) indicates that the *S. verecunda* complex, like the rest of the genus, is relatively slow to accumulate genetic synapomorphies at loci traditionally used for phylogenetic inference. Adopting a metapopulation view of monophyletic species circumscription (De Queiroz 2007) has recently increased in popularity because it can accommodate a greater number of natural processes, including ones causing reticulate patterns of evolution like hybridization and introgression. However, as Baum (2009) points out, monophyly is a feature of taxa that
arises after metapopulation lineages have been isolated for sufficiently long enough to accumulate fixed mutations. Given the lack of resolution in *Silene* phylogeny estimates to date (e.g., Oxelman et al. 1997; Popp and Oxelman 2004, 2007; Popp et al. 2005; Petri and Oxelman 2011), a ‘long time’ in *Silene* may be relatively much longer than in other Angiosperm lineages. It is not possible for us to evaluate Baum’s (2009) concepts of predictive power or robustness for *S. krantzii* at this time due to a paucity of genetic data, but recognition of this new species does have biological significance, utility, and precedent (Baum 2009). *Silene krantzii* is ecologically distinct from *S. verucunda*, occurs sympatriically only with another phylogenetically distant *Silene* species (*S. parishii* S. Watson), and can be distinguished phenotypically from putative close relatives. Additionally, we argue that there is taxonomic precedence for species recognition of *S. krantzii* despite the fact that putative close relatives have been previously treated both as separate species (Watson 1875, 1882, 1888; Jepson 1914; Clokey 1939) and subspecies (Jepson 1914, Hitchcock and Maguire 1947) of *S. verucunda*. All of the subspecies of *S. verucunda* treated by Hitchcock and Maguire (1947) were described as unique species in previous works (Watson 1875, 1882; Clokey 1939). Preliminary genetic evidence from nuclear and chloroplast loci suggest that numerous monophyletic taxa exist in the *S. verucunda* complex (T. Stoughton et al., Rancho Santa Ana Botanic Garden, unpublished data), including but not limited to all of the subspecies previously recognized by Hitchcock and Maguire (1947) included in our key (Appendix II). Additionally, botanists who are familiar with the *S. verucunda* complex have confirmed that this ‘species’ has served as a taxonomic dumping ground for numerous entities possessing some, but not all, of the diagnostic morphology of *S. verucunda* S. Watson (D. Taylor, Jepson Herbarium, personal communication). These taxa may be the products of recent, rapid radiation following hybridization and allopolyploidization (Petri and Oxelman 2011), but the signature is phenotypic diversification with minimal corresponding genetic change. Lest this phenotypic polymorphism be mistaken for plasticity, it should be noted that *S. krantzii* is supported by genetic synapomorphies, albeit extremely few at present, and a pilot common garden study in which phenotypic differences among *S. krantzii* and *S. verucunda* subsp. *platyota* from the San Bernardino Mountains were retained in flowering individuals (T. Stoughton, Rancho Santa Ana Botanic Garden, unpublished data).

Does the circumscription of *S. krantzii* represent one more slice in the *ad nauseum* splitting process of micro-taxonomists? Perhaps! Before elucidating the reasons why we think it is not only beneficial but our responsibility to recognize *S. krantzii* as distinct from *S. verucunda* s.l., we briefly discuss the negative aspects of so-called ‘taxonomic splitting’. Philosophically, it is undesirable to reduce species phylogenetically to their elements (i.e., genotypes). Species are meant to represent groups of individuals that share synapomorphies (shared, derived characters) rather than subgroups sharing particular alleles (i.e., genotypes). Recognizing genotypes as species predictably leads to species breakdown as a result of sexual reproduction and gene flow, and underestimation of intraspecific genetic diversity. From a conservation standpoint, taxonomic splitting may lead to increased, positive efforts to conserve particular species assemblages based on species richness. However, overestimates of richness due to taxonomic splitting may result in the conservation of certain genotypes rather than the species containing them (Zachos 2013). Conservation efforts based on inaccurate species circumscription resulting from overzealous taxonomic splitting could create a genetic bottleneck, which would then artificially put the species at very high risk. That said, a survey by Morrison et al. (2009) indicated that taxonomic splitting, relative to ‘lumping’ or making no taxonomic change, has produced only positive effects, increasing
awareness of particular groups and increasing their protection as well.

Disintegration of S. verecunda s.l. seems eminent and arguably represents taxonomic splitting. However, as our ability to understand phylogenetic relationships among taxonomic entities increases, our ability to understand morphological evolution and geographic distributions increases in turn. We think that it is our responsibility as taxonomists not only to circumscribe S. krantzii as distinct based on the evidence laid out in this study, but to learn everything we can about its natural history, testing its taxonomic status with new data when it is available. To this end, we hope that recognition of the narrowly endemic S. krantzii at the species level will also catalyze a re-evaluation of conservation needs for the entire S. verecunda complex. Although synonymized by Hartman et al. (2012) in the current treatment of The Jepson Manual, the infraspecific taxon Silene verecunda subsp. verecunda is still recognized as a rare plant (Rank 1B.2 — plants rare, threatened, or endangered in California and elsewhere; moderately threatened in California) by the California Native Plant Society (CNPS 2013).

**Biogeography**

The San Bernardino Mountains make up a floristically and geologically diverse region of significant botanical importance (Krantz 1994). San Gorgonio Mountain was the southernmost glaciated peak in western North America (Sharp et al. 1959, Owen et al. 2003) and consequently represents the southernmost limit of several widespread alpine plant taxa (Krantz 1994). A vast majority of high elevation (i.e., >3,000 m) areas in the San Bernardino Mountains are designated by the San Bernardino National Forest as the San Gorgonio Wilderness, the only place that Silene krantzii is currently known to occur. Krantz (1994) reviewed the vascular plant flora of the San Bernardino Mountains, citing nearly 1,600 taxa native to this region. Nineteen flowering plant species that grow in the alpine zone of San Gorgonio Mountain (ca. 40% of the total number of species surveyed by Krantz) are not found elsewhere in the San Bernardino Mountains but occur more widely to the north (Krantz 1994). With this study we add one additional species, increasing our knowledge of the endemic flora (ca. 8%) of the very rich and interesting summit region of San Gorgonio Mountain.

The geographic range of S. krantzii is intriguing given the distribution of other taxa in the S. verecunda complex (Figure 2). Other subspecies of Silene verecunda s.l. in the southwest U.S. include S. verecunda subsp. platyota, a common understory component in pine forests at lower elevations (<3,000 m) in the San Bernardino Mountains, and S. verecunda subsp. andersonii, a more xeric-adapted taxon that grows in the desert mountains, primarily to the northeast and not overlapping in distribution with S. krantzii. As mentioned previously, preliminary molecular assays suggest that S. krantzii is distantly related to S. verecunda subsp. andersonii and that other subspecies in the S. verecunda complex appear to be unique evolutionary lineages (Popp and Oxelman 2007; Petri and Oxelman 2011; T. Stoughton et al., Rancho Santa Ana Botanic Garden, unpublished data). Silene krantzii has been found only around the summit region of San Gorgonio Mountain thus far, but we recommend looking for this species on adjacent high peaks in southern California, particularly in the White Mountains of Inyo County, and the nearby San Gabriel Mountains (San Bernardino and Los Angeles counties) to the west. In the higher elevations of the eastern San Gabriel Mountains, Philip Munz collected individuals from “little baldy” that resemble S. krantzii (Munz 6119, POM13373 and UC218196) but differ in that they do not have leaves of reduced
size or a low-statured, spreading habit. The Munz collection also has inflorescences that are strict dichasia, more similar to those typical of S. verecunda subsp. playota. This and other collections from the higher elevation habitats in the San Gabriel Mountains did not escape the attention of Hitchcock and Maguire (1947) during preparation of their monograph on North American Silene, but ultimately they did not offer a name.

Silene krantzii may represent just one example of many plant lineages in southern California that have become widely disjunct from close congeners in the southern Rocky Mountains during the Pleistocene, as explained by the hypothesis of Major and Bamberg (1967) and others (e.g., Morefield 1992, Krantz 1994). The hypothesis of Cordilleran disjunction, sensu Major and Bamberg (1967), has been rejected by some authors (e.g., Chabot and Billings 1972, Raven and Axelrod 1978) who have instead favored more direct north to south dispersal along the Sierran-Cascadian axis. Although S. krantzii is currently known only from the San Bernardino Mountains, the preponderance of examples of other species on San Gorgonio Mountain would lend support to either of the two competing hypotheses. Many widespread species that inhabit the alpine zone on San Gorgonio Mountain occur also in the alpine habitats of the eastern Sierra Nevada and White Mountains of California (Morefield 1992, Krantz 1994). Discontinuous populations of these plants are spread across the Basin and Range Province linking populations in the western mountain ranges to populations in the southern Rocky Mountains (Major and Bamberg 1967, Morefield 1992, Krantz 1994). Therefore, locating additional populations of S. krantzii and an understanding the phylogenetic relationship of this new species by others will be essential for developing hypotheses regarding its origin and evolution over time.

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Literature Cited


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APPENDIX I: LIST OF VOUCHER SPECIMENS OF *SILENE KRAKANZII* AND *S. VERECUNDA* EXAMINED FOR THIS STUDY

USA, California, Desert Mountains District (including White and Inyo Mountains),
Inyo and San Bernardino Counties: *S. verecunda subsp. andersonii* specimens. —
RSA296490, Castagnoli 198, 6 Jun 1980; RSA624136, DeDecker 3310, 27 Jul 1973;
RSA270672, Henrickson 13986, 13 May 1974; UC1549855, Morefield 4148, 18 Jul
1986; RSAA46336, Morefield 4804, 19 Jul 1988; RSA352210, Peterson 601, 15 Jun
1982; RSA552077, Romspert 425, 11 Aug 1977; RSA290816, Thorne 44874, 10 Jul 1974;
RSA334384, Thorne 54802, 21 Sep 1980.

USA and MEX, California (including Baja), Sierra Nevada, Transverse Ranges, and
Peninsular Ranges Districts, Fresno, Kern, Los Angeles, Orange, Riverside, San Bernardino,
and Tulare Counties: *S. verecunda subsp. platyota* specimens.—RSA507942, Boyd 2260,
RSA438862, Davidson 2978, 3 Jul 1975; UC1618234, Ertert 6311, 9 Jun 1986; RSA727590,
Fraga 735, 19 May 2003; RSA727455, Fraga 1265, 18 Jun 2004; RSA680009, Gross 1020,
10 Jun 2003; RSA795882, Gross 5573, 11 Jul 2012; RSA225227, Moran 14479, 21 Aug
1967; RSA659142, Moran 28862, 21 Jun 1980; RSA679167, Roberts 5936, 25 Jun 2003;
RSA546449, Ross 3063, 2 Jul 1990; RSA637501, Soza 514, 10 Jun 1999; RSA682367,
Soza 1701, 25 Jun 2003; RSA599719, Swinney 3942, 29 Jun 1995; RSA596614, Swinney
3974, 6 Jul 1995; RSA733088, Swinney 7994, 20 Jun 2001; RSA774867, Swinney 11253,

USA, California, Coast Ranges and San Francisco Bay Area Districts, Monterey,
San Benito, San Francisco, San Louis Obispo, and Santa Cruz Counties: *S. verecunda subsp.
verecunda* specimens.—JEPS102187, Douglas HL369b, 20 May 1994; UC1583623, Keil
20704, 11 Jun 1988; RSA330449, Norris 4829, 14 Mar 1985; JEPS81534, Stone 462, 13
May 1982; RSA502348, Taylor 9617, 29 Apr 1988; JEPS90790, Taylor 11942, 30 Jun

**APPENDIX II: KEY TO THE S. VERECUNDA SPECIES COMPLEX**

1. Flowering calyx somewhat inflated (slightly at times), generally reddish in color,
lobes (teeth) keeled or not; basal leaves generally (5)-8-60 mm long

   2. Alpine (high elevation) habitats, trichomes glandular on proximal-most
leaves; flowering calyx lobes generally strongly keeled; inflorescence a monoashington,
branches spreading to ascending .................................................. *S. krantzii*

   2' Coastal (low elevation) habitats, at least some non-glandular trichomes on
petioles of proximal-most leaves; flowering calyx teeth generally not keeled; inflorescence
a compound dichasium (occasionally simple, sometimes monochasial below), branches
ascending to erect ................................................................. *S. verecunda subsp. verecunda*

1' Flowering calyx tubular, generally greenish in color (rarely reddish), lobes (teeth)
not keeled; basal leaves generally 60-100 mm long (sometimes withering early)

   3. Proximal-most leaves sparsely minute-glandular with noticeably
thickened midribs or marcescent bases, generally withering early; transmontane pine and
oak woodlands; inflorescence a monoashington (rarely dichasial) ........................................
................................................................................................. *S. verecunda subsp. andersonii*

   3' Proximal-most leaves generally non-glandular (if glandular, then not
sparsely so) and lacking noticeably thickened midribs or marcescent bases, not withering
early; generally cismontane pine and oak woodlands; inflorescence a dichasium (sometimes
monochasial below) ................................................................. *S. verecunda subsp. platyota*